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Task relevance differentially shapes ventral visual stream sensitivity to visible and invisible faces

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Abstract

Top-down modulations of the visual cortex can be driven by task relevance. Yet, several accounts propose that the perceptual inferences underlying conscious recognition involve similar top-down modulations of sensory responses. Studying the pure impact of task relevance on sensory responses requires dissociating it from the top-down influences underlying conscious recognition. Here, using visual masking to abolish perceptual consciousness in humans, we report that functional magnetic resonance imaging (fMRI) responses to invisible faces in the fusiform gyrus are enhanced when they are task-relevant, but suppressed when they are task-irrelevant compared to other object categories. Under conscious perceptual conditions, task-related modulations were also present but drastically reduced, with visible faces always eliciting greater activity in the fusiform gyrus compared to other object categories. Thus, task relevance crucially shapes the sensitivity of fusiform regions to face stimuli, leading from enhancement to suppression of neural activity when the top-down influences accruing from conscious recognition are prevented.

Key words: FFA; fMRI; subliminal perception; attention

Neuronal activity in visual cortex reflect the interplay between bottom-up processing of sensory inputs and top-down influences from higher-order regions such as the prefrontal cortex (Corbetta and Shulman 2002; Gilbert and Li 2013). One major source of top-down modulation reflects the current task relevance, promoting sensory representations that are behaviourally relevant at the expense of competing irrelevant information (Desimone and Duncan 1995; Peelen et al. 2009; Peters et al. 2012). However, characterizing the impact of task relevance on visual regions remains challenging, because the mere recognition of a stimulus, regardless of task relevance,

involves perceptual inferences that also influence sensory responses via top-down modulations (Mumford 1992; Ullman 1995; Friston 2005; Gilbert and Sigman 2007). Specifically, whenever bottom-up signals accumulate enough to cross a threshold, top-down mechanisms are triggered, allowing for the amplification and maintenance of sensory information in visual cortex and the concomitant elaboration of a conscious perceptual representation (Dehaene and Changeux 2011). Since perceptual inference might prompt participants to focus on task-irrelevant information (e.g. a familiar face while searching for alternative objects), previous studies may have, thus, unwittingly

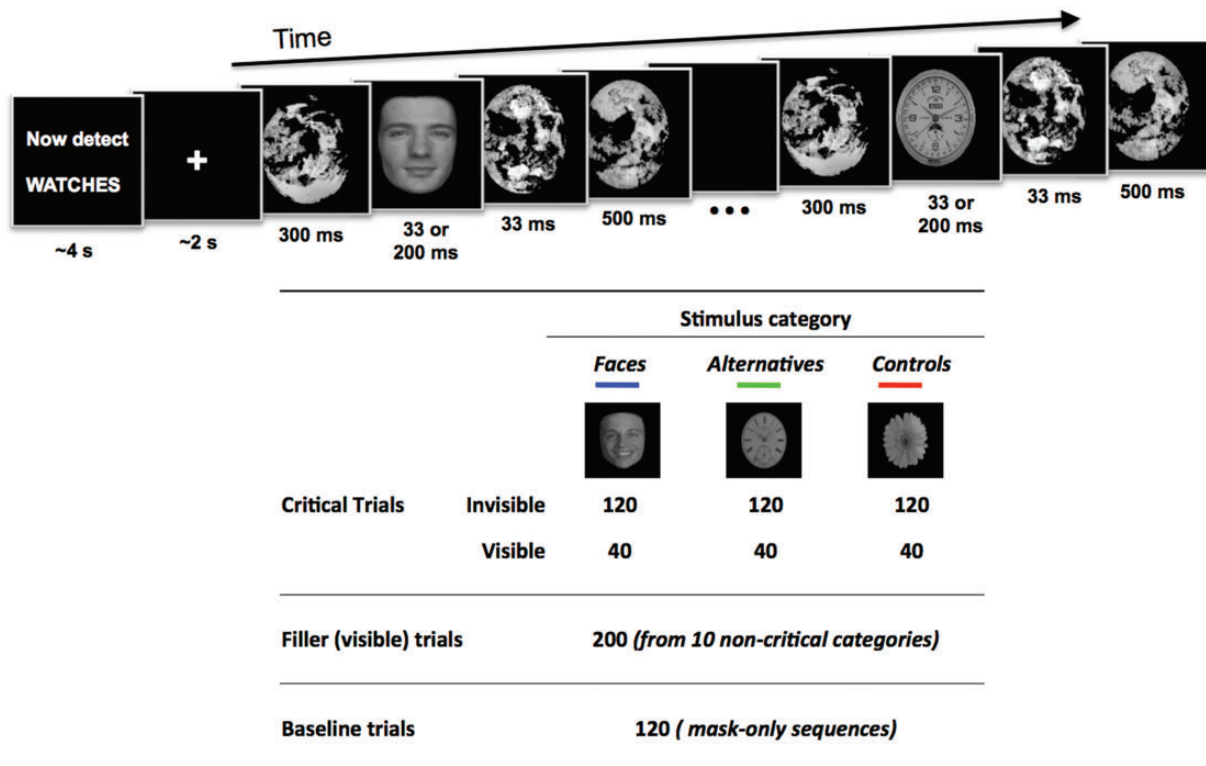


Figure 1. Experimental procedure. Participants viewed images of faces, watches and flowers presented under visible or invisible conditions (200 ms vs. 33 ms, respectively). Task relevance was varied across interleaved blocks of 20 trials, with the instruction to detect only faces or to detect only alternatives (watches or flowers, counterbalanced across subjects). A third category of stimuli (flowers or watches, respectively) that was never task-relevant served as a control condition. These critical objects were interspersed which filler stimuli presented consciously and belonging to a large number of categories (balls, burgers, cars, cups, donuts, fruits, guitars, hats, snails, wheels). Baseline (mask-only) trials containing no object were also used to account for overall baseline shifts across task relevance.

confounded these two distinct sources of top-down influences (O'Craven et al. 1999; Summerfield et al. 2006).

A potential solution to this issue consists in studying how task relevance shapes sensory responses during non-conscious processing stages, prior to the elaboration of a conscious percept. Non-conscious processing occurs when sensory signals are rendered invisible, usually through visual masking, but continue inducing influences at both neural and behavioural levels (Breitmeyer and Ogmen 2006; Kouider and Dehaene 2007), without exciting the re-entrant processing characteristics of conscious perception (Lamme and Roelfsema 2000; Dehaene and Changeux 2011). For instance, the fusiform face area (FFA)—an extrastriate region within the ventral visual stream with neurons preferentially tuned to faces (Kanwisher et al. 1997)—remains responsive to faces even when they are rendered fully invisible by masking (Morris et al. 2007; Kouider et al. 2009; Fahrenfort et al. 2012). Yet, it remains unclear whether FFA responses to invisible faces can be biased by task relevance.

To address this issue, we measured fMRI BOLD responses in the FFA to faces and non-face objects that were either visible or invisible, and either task-relevant or task-distracting (Fig. 1). Participants made category-specific detection judgements by pressing a button only for faces in face detection blocks, and only for alternative objects (e.g. watches) in alternative detection blocks. Thus, face stimuli and alternative objects were in turn task-relevant or task-distracting across blocks. This design allowed us comparing whether FFA responses to invisible stimuli are exclusively influenced by stimulus category (i.e. stronger

response for faces regardless of the task relevance) or rather dependant on task relevance (i.e. stronger response for faces only when this category is task-relevant). In the latter case, the use of an additional control category (e.g. flowers) that was never task-relevant throughout the experiment allowed us to test whether task-distracting faces are simply ignored (i.e. filtering of FFA responses) or actually inhibited (i.e. suppression of FFA responses; Fig. 2).

Methods

Subjects

A total of 20 healthy volunteers (12 females, age 24 ± 5 years, all university students) gave written consent to participate in the study. All volunteers were right-handed, had normal or correct-to-normal vision and were in good health, with no history of psychiatric or neurological illness. The protocol of this study was approved by the local ethical committee (CPP 71-07, Pitié-Salpêtrière, Paris, France).

Stimuli

The stimuli were greyscale photographs of 180 faces, 180 flowers and 180 watches serving as critical stimuli, in addition to 200 filler stimuli equally balanced across 10 categories (balls, burgers, cars, cups, donuts, fruits, guitars, hats, snails, wheels). Stimuli across the different categories were matched for image size, as well as for average luminance and contrast. The faces

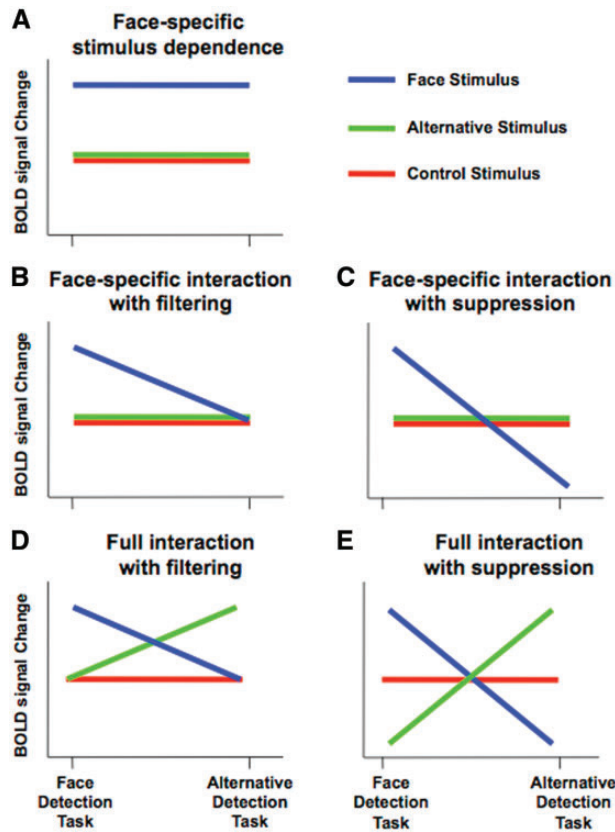


Figure 2. Predictions of BOLD responses in the FFA to invisible faces and objects as a function of task relevance by five models of interest (see 'Methods' section). Our results provide support for hypothesis C, involving face-specific interactions with suppression.

(half male, half female) were unknown to the participants and the pictures were cropped to show face only. Watches were all analogical, old or new style, and were cropped to show only the display part. Flowers and filler objects were selected with the constraint that they would lead to a round or elliptical form after cropping them from their background. If necessary, stimulus shape was modified to convey curved borders, leading roughly to a round or elliptical form. This manipulation was performed to ensure masking efficiency, the masks being round/elliptical. Each mask was created using Adobe Photoshop by blending 6 randomly chosen images from the 3 critical categories together (2 upside-down faces, 2 watches, 2 flowers), resulting in non-informative patterns (Fig. 1). The average luminance and contrast of the masks were set to be similar to those of the stimuli.

Procedure and design

Participants received the following stimulus sequence on each trial: a forward mask presented for 300-ms, the target stimulus for either 33-ms (invisible condition) or 200-ms (visible condition), a first backward mask for 33-ms and then a second backward mask for 500-ms. The target stimulus could either be a face, an alternative stimulus (flower or watch, counterbalanced across participants), a control stimulus (watch or flower, respectively) or a filler stimulus. All stimuli were presented foveally, with a width of 3° and a height of 4°. Participants could also receive mask-only trials (baseline condition) in which no target was presented but a blank screen for the same duration as the

invisible targets (i.e. 33-ms). Participants received blocks of 20 trials, with an inter-trial interval of 2.6 s. Note that the repetition time of the fMRI sequences (i.e. the TR, or time interval between successive excitation pulses applied to the same slice) differed from the inter-trial interval and was set to 2.08 s, allowing us to better model the BOLD response in this event-related design. Each block started either with the instruction 'Now detect FACES' or, depending on the participant, with the instruction 'Now detect WATCHES' or 'Now detect FLOWERS' with the stimulus category displayed in specific colours (cyan or yellow, representing either faces or alternatives, counterbalanced across participants). This instruction lasted about 4 s (i.e. 2 TRs of the fMRI sequence, see below) and was followed by a fixation cross also presented for 2 TRs. Each block was followed by an additional resting period where only the fixation cross appeared for about 15 s (7 TRs). The participant's task was to press a button, as quickly as possible, when they saw a stimulus corresponding to the instructed category. They were encouraged to use a liberal criterion (respond even in the absence of full certainty regarding the stimulus category). Participants were also instructed to be careful in respecting the instructions (i.e. avoid responding to categories other than the instructed category). To minimize the possibility that subjects would be confused regarding the instructed category, stimuli were framed in empty rectangles with thin lines coloured in cyan or yellow such as to match their respective task. This assignment of colours to categories was counterbalanced across subjects. Participants received a total of 40 blocks of 20 trials, alternating between the two tasks from one block to another, and resulting in a total of 800 trials (see Fig. 1). The trial list consisted of (i) 360 subliminal trials with faces, alternatives and control stimuli ($N = 120$ for each category, 15% of the total); (ii) 120 visible critical trials that were also distributed across the face, alternative and control categories, but in a smaller proportion ($N = 40$ for each category, 5% of the total); (iii) 200 filler stimuli (25% of the total); and (iv) 120 baseline mask-only trials (15% of the total). The whole experiment was broken down into 5 fMRI sessions of 8 blocks each, resulting in 160 trials per session. Accordingly, each fMRI session contained a balanced proportion corresponding to a fifth of the trial list (i.e. 72 subliminal trials, 24 visible critical trials, 40 filler stimuli and 24 baseline trials). The filler and baseline trials were interleaved with the subliminal and visible critical trials. Thus, for a given block of 20 trials (i.e. corresponding to a specific task instruction) the target could be any stimulus (i.e. either a face, a flower, a watch, a filler, or a mask-only trial). Furthermore, the trial order was randomized within each session of 160 trials, except for the balancing of stimulus conditions across the two types of blocks (i.e. tasks sets). This randomization within a session rather than within a block ensured that participants constantly paid attention to the stimulus sequence, since they could not predict the number of (visible) targets within a block.

fMRI data acquisition and analysis

Imaging was performed with a Siemens (Erlangen, Germany) Allegra 3T scanner to obtain gradient echo T2*-weighted echoplanar images with blood oxygenation level-dependent contrast as an index of local increases in synaptic activity. Data are available on request. The image parameters used were as follows: matrix size, 64×64 ; voxel size, $3 \times 3 \times 4$ -mm; echo time, 30-ms; repetition time, 2080-ms. Imaging data were analysed with SPM5 (Wellcome Department of Cognitive Neurology, London, UK). Prior to pre-processing, five initial volumes were discarded to eliminate non-equilibrium effects of magnetization. For each

subject, functional images were slice-time corrected and spatially realigned to the first volume acquired. Transformation parameters were derived from normalizing the coregistered mean echo planar image to a corresponding template brain within the stereotactic space of the Montreal Neurological Institute. The derived parameters were then applied to normalize the remaining echo planar volumes for that subject. Normalized images were resampled at 3-mm^3 then smoothed with a Gaussian kernel of 8 mm^3 full-width half-maximum. Temporal correlations were estimated using restricted maximum likelihood estimates of variance components using a first-order autoregressive model. The resulting non-sphericity was used to form maximum likelihood estimates of the activations. For the statistical analysis of the main experiment, we first constructed, for each participant, a model with 16 regressors $\{[(3 \text{ stimulus categories} \times 2 \text{ visibility conditions}) + \text{baseline} + \text{fillers}] \times 2 \text{ task relevances}\}$ that were convolved with a canonical haemodynamic response function and its time and dispersion derivatives. We then extracted the 12, baseline-corrected images (i.e. by subtracting the mask-only trials) consisting in the 12 conditions of interest and corresponding to our experimental design of 3 stimulus categories, 2 visibility conditions and 2 task relevances.

This design allowed us to compare five models of interest regarding the nature of FFA responses to invisible objects, ranging from exclusive dependence on face-specific stimulation to full interactions between object category and task relevance (Fig. 2). Indeed, a first model of 'Face-specific stimulus dependence' predicts that invisible faces automatically and mandatorily trigger response in the FFA and remain unaffected by task relevance, resulting in increased activity for faces compared to other objects regardless of the task relevance (Fig. 2A). Models of 'Face-specific interactions' also predict that fusiform responses remain primarily sensitive to faces, but now through the combination of stimulus and relevance, leading to FFA increase only for face stimuli presented during a face task. Two instances can be derived from this account: one with 'filtering', in which task-irrelevant faces have no influence on the FFA (Fig. 2B) and one with 'suppression' in which FFA responses are actually suppressed for task-irrelevant faces (Fig. 2C). Finally, models of 'Full interaction' predict that FFA responses are not specific to face stimuli but instead primarily depend on the interaction between stimulus category and task relevance. This account predicts increased responses for face stimuli only when attending faces and for alternative stimuli only when attending the alternative category. Here also, the alternative stimulus, when it becomes task-irrelevant, can either be filtered out (Fig. 2D) or actively suppressed (Fig. 2E).

Localizer

The FFA (Kanwisher et al. 1997) was mapped in each participant by a subsequent localizer run comparing images of faces with that of flowers and watches. Stimuli from the 3 categories were presented in a blocked design [20 stimuli/block, each presented for 750-ms with an inter-stimulus interval of 1000-ms, and with about 10s (5 TRs) of fixation baseline between blocks]. Participants performed a 1-back repetition detection task on the stimuli (with 3 stimulus repetitions occurring at random positions within each block of 20 trials), by pressing a button whenever two identical stimuli were presented in a row. Preprocessing and statistics were analogous to the main experiment, except that only a canonical HRF was used for this fully block-based design. For each of the participants, we isolated face-sensitive voxels on the bilateral fusiform gyrus, by

contrasting BOLD responses to faces compared to the other objects at an uncorrected threshold of $P < 0.0001$. In each subject and each of the 12 conditions of interest, we then averaged per cent signal change within this cluster for further ANOVAs and planned pair-wise *t*-tests (two-tailed). For illustration purpose, Fig. 3A displays the bilateral FFA cluster obtained from a group-level (random effect) analysis on this contrast, using the same uncorrected threshold of $P < 0.0001$.

Results

The overall task performance on the visible objects was high with a mean accuracy of 96.1% (SD = 3.6%), revealing that participants were fully able to respond to stimuli from the target category while ignoring the distracting ones. Accuracy did not differ according to whether the target category was that of faces or the alternative (97.1% vs. 95.3%, $t_{(19)} = 1.43$, $P = 0.17$). In contrast, participants only rarely responded to the invisible objects (less than 1% of the trials) and, when they did so, failed to distinguish between targets and other objects ($d' = 0.024$, *t*-test against zero, $t < 1$), confirming that they could not identify stimuli in the invisible condition. This result is consistent with the previous studies reporting null sensitivity in face discrimination tasks using similar masking parameters (Gelskov and Kouider 2010; de Gardelle et al. 2011).

One potential issue with the current protocol, which involves a go-no go decision, is that the criteria used to report a target might be affected by subjects responding only rarely to target stimuli. One might thus argue that subjects saw the stimuli even in the invisible condition, but did not consider these trials with low visibility as task relevant. To verify that perceptual awareness was genuinely impossible in the invisible condition, we instructed a new group of subjects ($N = 10$; tested outside the scanner) to either perform the exact same task during half of the visibility test, or to perform a more standard, non-speeded category discrimination task in which subjects were forced to respond on every trial (i.e. forced-choice yes-no discrimination task), during the other half of the visibility test (order counterbalanced across subjects). Here also, they received 360 subliminal trials with faces, alternatives and control stimuli ($N = 120$ for each category); and 120 visible trials ($N = 40$ for each category), in addition to 160 fillers (the baseline mask-only trials were removed for this test). This visibility control confirmed that under such presentation conditions, the stimuli in the invisible conditions could not be discriminated not only when responding solely to the target category ($d' = 0.061$, $t < 1$), but also when performing a forced-choice on each trial ($d' = -0.013$, $t < 1$).

Focussing our imaging analyses on the FFA defined by the independent localizer scan, we found that FFA responses were significantly modulated by visibility, stimulus category, and task relevance, as indicated by the presence of a significant three-way interaction $[2 \text{ (visibility)} \times 3 \text{ (stimulus category)} \times 2 \text{ (task relevance)}]$ factorial repeated measures ANOVA; $F_{(2, 38)} = 4.31$, $P = 0.02$. In the following, we examined the impact of task relevance on FFA responses to different stimulus categories in the absence or presence of perceptual consciousness.

Task-related enhancement and suppression for invisible faces

We first studied FFA activations in the invisible condition as a function of task relevance and stimulus category. We extracted parameter estimates for the invisible (i) faces, (ii) alternative

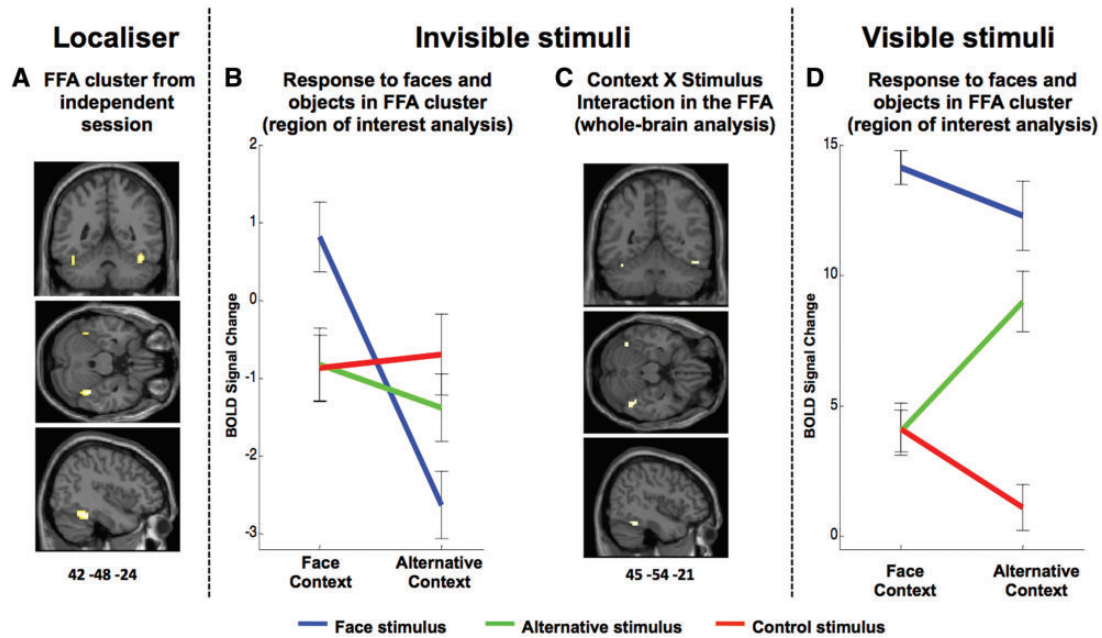


Figure 3. (A) FFA localization obtained in a localizer session subsequent to the main experiment. The FFA cluster was obtained by running a group-level analysis on activations elicited by faces vs. other (flowers/watches) objects in a one-back repetition detection task (at $P < 0.0001$). (B and D) Average parameter estimates (\pm within-subject SEM) obtained from the FFA localizer as a function of stimulus category (face, alternative, control) and task relevance (face vs. alternative task detection) for the invisible (B) and visible (D) trials. (C) Group-level analysis for the interaction between faces vs. other (i.e. alternative/control) objects and face vs. alternative task detection, thresholded at an uncorrected $P < 0.001$ (left FFA peak MNI coordinates, $x = -39$, $y = -57$, $z = -24$; right FFA peak, $x = 45$, $y = -48$, $z = -24$).

objects and (iii) control objects, under both the face detection and the alternative detection tasks. A 3 (stimulus category) \times 2 (task relevance) factorial repeated measures ANOVA (Fig. 3B) failed to reveal a main effect of task relevance ($F_{(1, 19)} = 1.23$, $P = 0.28$) or stimulus category ($F_{(2, 38)} = 0.14$, $P = 0.87$). However, crucially, we found a robust stimulus \times task interaction on FFA parameter estimates ($F_{(2, 38)} = 6.75$, $P = 0.003$). Further analysis revealed that FFA responses to faces were enhanced during face relevance blocks relative to alternative relevance blocks ($t_{(19)} = 2.82$, $P = 0.01$), whereas there was no significant effect of task relevance for the other objects, neither for alternative stimuli ($t_{(19)} = 0.43$, $P = 0.67$) nor for control stimuli ($t_{(19)} = -0.13$, $P = 0.90$). To assess more directly whether neural activity in the FFA was selective to faces, we compared responses induced by invisible face stimuli and responses induced by the other invisible objects (i.e. collapsing the alternative and control conditions). Interestingly, while the FFA responded more to invisible faces than to the other invisible objects in the face detection blocks ($t_{(19)} = 2.74$, $P = 0.01$), the converse was true in alternative detection blocks: FFA activity to invisible faces was now reduced relative to other invisible objects ($t_{(19)} = -3.11$, $P = 0.006$). Further analysis in the face-relevant condition showed that the activity for invisible faces was amplified relative to either invisible alternative objects ($t_{(19)} = 2.246$, $P = 0.037$) or to invisible control objects ($t_{(19)} = 2.237$, $P = 0.038$). Restricted comparisons in the alternative relevance condition revealed that although the contrast of faces $>$ alternative objects did not reach significance ($t_{(19)} = -1.59$, $P = 0.13$), invisible faces led to a reduction in activity relative to invisible control objects ($t_{(19)} = -3.09$, $P = 0.006$). Furthermore, there was a significant reduction of activity when considering FFA activity to invisible faces relative to the baseline activity set by the mask-only trials ($t_{(19)} = -3.06$, $P = 0.007$). These results imply that FFA responses to

invisible, task-distracting, face stimuli were not only reduced but actually suppressed in that situation. This pattern provides evidence for the model of 'Face-specific interactions with suppression' (compare Figs. 2C and 3B). In addition, these findings with invisible stimuli were confirmed when the stimulus (face vs. alternative and control objects) \times task (face vs. alternative relevance) interaction was assessed in a voxelwise fashion across the whole brain, revealing bilateral clusters on the fusiform gyrus (Fig. 3C). These findings reveal that in the absence of top-down modulations triggered by perceptual recognition of the stimulus itself (i) the FFA is sensitive to the presence or absence of a face, but not the presence or absence of alternative or control object categories; (ii) however, there is no global advantage for faces over other object categories in driving the amplitude of the BOLD signal in the FFA, in this situation where perceptual consciousness is abolished; (iii) FFA responses to faces were enhanced compared to other object categories when faces were task-relevant, but suppressed when faces were task-irrelevant.

Task-related modulations during conscious perception

To address whether this pattern was specific to invisible stimuli, we performed the same analysis on visible stimuli (Fig. 3D). We found a significant main effect of stimulus ($F_{(2, 38)} = 25.76$; $P < 0.0001$), as well as a significant stimulus \times task relevance interaction ($F_{(2, 38)} = 4.47$; $P < 0.02$). The FFA response to faces did not differ between the face detection task and the alternative task ($t < 1$). Yet, there was marginal advantage for faces over alternative objects in the face task compared to the alternative task ($F_{(1, 19)} = 4.12$; $P = 0.057$). These results confirm that in the presence of perceptual consciousness, FFA responses are modulated by task relevance (O'Craven et al. 1999;

Summerfield et al. 2006; Peters et al. 2012). Yet, our data also reveal that, compared to the unconscious condition, this task-related modulation is less stringent for faces since FFA responses remain stronger for visible faces compared to other objects regardless of their relevance (i.e. even when faces are task-distracting). Actually, we found that, if anything, FFA responses to the alternative stimulus category were primarily affected by task relevance. Indeed, when comparing the alternative and control category, we observed a significant interaction with task context ($F(1, 19) = 11.31$; $P < 0.005$). This reflected a stronger FFA response for the alternative stimulus category when relevant (i.e. in alternative relevance blocks) compared to the control category ($t(19) = 8.394$, $P < 0.001$), while FFA responses were virtually identical in face relevance blocks ($t < 1$; see Fig. 3D). Along the same lines, comparison across the two task contexts revealed a significant difference for the alternative stimulus category ($t(19) = -3.237$, $P < 0.005$), but not for the control category ($t < 1$). This suggests that, under conscious processing conditions, the FFA is not only responsive to non-face stimuli to some extent, but also that this response is amplified when the non-face objects are task-relevant.

Altogether, our results confirm that task relevance and perceptual consciousness interact with each other in shaping category-specific responses in visual cortex. Yet, they also reveal that task relevance can lead to a full suppression and reversal of neural activity when top-down influences accruing from conscious recognition are prevented.

Discussion

This study aimed at testing how task-related information impacts neuronal activity in sensory regions in the presence or absence of perceptual consciousness. While responses to visible faces are known to be modulated by task relevance (O'Craven et al. 1999; Summerfield et al. 2006), we set out to characterize how task relevance shapes the processing of faces rendered invisible by visual masking (Morris et al. 2007; Kouider et al. 2009). Interestingly, we found that task relevance differentially modulates neural activity in the FFA associated with visible and invisible faces. As expected, visible faces elicited greater activity in the FFA compared to other stimulus categories, and this response was enhanced when faces were task-relevant. However, a distinct pattern of task-related modulation was observed for invisible faces: invisible faces elicited greater neural activity in the FFA when task-relevant, but were suppressed when task-irrelevant and distracting, resulting in a reduced activity for faces over other stimuli in the FFA. Interestingly, the pattern of activity observed in the FFA remained selective for faces, even if the direction of the effect diverged according to task relevance. It is of note that this specific deviation of the BOLD signal for faces (whether positive or negative) argues against a simple additive effect of task relevance on sensory responses. In contrast to models assuming a monolithic accumulation process (Gold and Shadlen 2007; Ratcliff and McKoon 2008; Kiani and Shadlen 2009), our results provide further support that decision-making mechanisms are impacted by conscious and unconscious sensory evidence in qualitatively distinct manners (Vlassova et al. 2014).

At first glance, the pattern of data we observed calls into questions the claim that the FFA is inevitably and automatically activated (i.e. above baseline) by the mere presentation of a face stimulus (Kanwisher and Yovel 2006; Kanwisher and Dilks 2014). Yet, it remains possible that faces automatically induce neural activations in the FFA, as suggested by the previous

studies (Moutoussis and Zeki 2002; Lavie et al. 2003; Finkbeiner and Palermo 2009; Fahrenfort et al. 2012), but that this automatic activation of the FFA is followed by a suppression of neural responses when invisible faces become task-distracting, as found in the present study. For instance, a recent study showed that although subjects performed a totally irrelevant task of ellipse localization, faces rendered invisible by binocular fusion still activated the FFA (Fahrenfort et al. 2012). Note, though, that even if faces were task-irrelevant in this study, they were intermixed with a certain proportion of visible faces, which might still bias participants' attention and expectations towards that category [see Gayet et al. (2014) for a similar argument]. Further studies might be able to fully disentangle this issue by investigating the neural impact of faces that are never task-relevant and never visible throughout the experiment.

One possibility might be that invisible stimuli are sufficiently processed to trigger top-down influences from higher-order areas, which would then either enhance or suppress sensory responses depending on task relevance. Recent studies confirmed that non-conscious stimulus processing is not necessarily restricted to perceptual systems, but can also trigger activations in prefrontal regions under certain circumstances, such as when cognitive control and executive functions are heavily involved. For instance, invisible cues, when mapped with task-switching operations, can modulate neural activity in premotor and inferior prefrontal cortices (Lau and Passingham 2007). Similarly, invisible stimuli associated with inhibitory, no-go responses in a go/no-go paradigm can provoke behavioural interference and involve the supplementary motor area associated with cognitive control (van Gaal et al. 2009; van Gaal et al. 2010). This region is also crucially involved in the unconscious control of actions and the inhibitory suppression of motor decisions (Boy et al. 2010a, 2010b). In our study, one possibility is that these anterior regions, in turn, might have sent top-down inhibitory signals towards sensory regions dealing with the irrelevant, task-distracting category (i.e. the FFA). Indeed, the suppression of FFA activity for irrelevant faces may be a consequence of our design in which participants were task-switching backwards and forwards between face and alternative detection tasks in a rapid block cycle. In other words, the automatized response execution for faces would persist even in blocks in which participants were instructed to detect alternative objects, and an invisible face would continue triggering an unconscious motor response that would need to be counteracted by cognitive control mechanisms all the way down to visual areas. A related possibility (Bar et al. 2006; Kveraga et al. 2007) might be that invisible faces induce a rapid bottom-up activation of prefrontal cortex through magnocellular pathways, which would in turn modulate neural responses in fusiform regions, here as a function of task relevance. Further studies should address the scope and limits of higher-order regions such as prefrontal cortex in triggering top-down modulations in the absence of consciousness.

By revealing that task relevance can modulate ventral visual stream activity for invisible faces, our study sheds new light on the dissociation between attention and consciousness (Koch and Tsuchiya 2007; Cohen et al. 2012). Indeed, a growing body of behavioural evidence has shown that, contrary to the idea that attention and consciousness go hand in hand, non-conscious perceptual processes can be modulated by temporal (Naccache et al. 2002) or spatial forms of attention (Montaser-Kouhsari and Rajimehr 2005; Jiang et al. 2006; Bahrami et al. 2008; Faivre and Kouider 2011). For instance, at the neural level, Bahrami et al. (2007) showed that retinotopic activity evoked in the primary

visual cortex (V1) to peripheral objects rendered invisible by interocular suppression is modulated by the attentional load in a foveal task. Our study goes further by revealing that selective attention, in the absence of awareness, involves not only response enhancement for task-relevant information, but also the active filtering of distracting information in visual cortex (Kastner and Ungerleider 2000; Carrasco 2011). A recent theory, termed the attentional sensitization model of unconscious cognition (Kiefer and Martens 2010; Kiefer 2012) proposes that various influences of executive control factors impact different forms of unconscious automatic processing. Interestingly, this model postulates that the attentional influences originating from task sets enhance task-relevant unconscious processes, congruent with our results. However, this model also postulates that the active inhibition of task-irrelevant information is confined to controlled processing of consciously perceived stimuli, more in accords with traditional accounts of automaticity (Posner and Snyder 1975; Neely 1977; Merikle et al. 1995). Our results disconfirm this latter aspect of the model by revealing active mechanisms of suppression can be extended to unconsciously perceived stimuli.

The observation of enhanced brain activity for task-relevant stimuli and suppression for task-distracting stimuli is partially consistent with a recent study (Seidl et al. 2012) who studied the impact of task relevance but used visible (non-face) objects and focussed on neuronal response in the entire object-selective cortex rather than on a category-specific cluster such as the FFA. In their study, Seidl et al. (2012) found enhancement for task-relevant objects and suppression for task-distracting objects, while we observed suppression in the FFA only when faces were invisible, not for visible ones (Fig. 3). One possibility might be that FFA responses to visible faces constitute a special case, in which the conscious perceptual representation induced by faces has a much stronger impact that overcomes the suppression due to task irrelevance. Indeed, faces have been argued to constitute an exceptionally salient category with a strong bias in terms of attentional focus (Vuilleumier 2000; Ro et al. 2001; Hershler and Hochstein 2005; Langton et al. 2008), which would explain why FFA activity induced by distracting faces cannot be fully suppressed when they become visible. Another possibility is that conscious recognition was in itself limited in the Seidl study since object pictures were barely visible, with task-relevant and task-irrelevant categories appearing (i) simultaneously on images of complex scenes, (ii) very briefly (i.e. 70-ms) and (iii) followed by a masking stimulus. Although stimulus awareness was not assessed in their paradigm, it remains possible that these challenging perceptual conditions limited top-down perceptual factors, allowing for a full interaction with task relevance. Of course, it still remains possible that the suppression we observed for task-distracting faces is not driven by top-down influences but rather by bottom-up mechanisms sensitive to stimulus duration (i.e. reflecting shorter presentation durations of 33-ms for invisible compared to the 200-ms visible stimuli). Similarly, one can argue that a duration-dependent go-no-go design might be at the origin of the differences we observed, rather than a genuine difference between unconscious and conscious processing conditions. Further experiments should rule out these possibilities, for instance, by showing a full reversal of FFA activity for task-distracting faces presented very briefly (33 ms) while remaining unmasked and visible.

In sum, the current study confirms that the FFA involves a preferential response to face over other objects even in the absence of perceptual consciousness, but reveals here that this category-specific sensitivity can be fully modulated by the task

relevance. Previous studies have demonstrated that invisible cues can activate posterior prefrontal areas dealing with cognitive control, whether these cues involve task-switching (Lau and Passingham 2007) or inhibiting motor responses (van Gaal et al. 2010). These studies converge to show that higher-order areas dealing with task relevance can be triggered in a non-conscious manner. The current study provides further evidence for the flexibility of non-conscious perceptual processes, by showing that sensory regions can in turn be modulated by task relevance. This suggests that the locus of neural suppression in the FFA, when faces are detrimental to the current task relevance, stands as a late component, rather than an early mechanism of filtering. Further studies investigating the temporal dynamics of the interplay between higher-order and sensory regions are needed to clarify this issue.

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